

LITTORAL HETEROGENEITY AND DIEL BEHAVIOR OF WHITE BASS (*MORONE CHRYSOPS*) AND CARP (*CYPRINUS CARPIO*) IN UTAH LAKE, UTAH

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ABSTRACT.—Diel activity and association patterns of white bass (*Morone chrysops*) and carp (*Cyprinus carpio*) in Utah Lake, Utah, were studied over four 24-hr periods during August 1980. Fish were concurrently sampled from two adjacent littoral habitats. Significant differences existed in diel activity patterns in two of three size classes of white bass and in diel association patterns of white bass and carp between the two habitat areas. Differences in habitat structure, and in biological activity between the habitat types, are implicated as the primary determinants of overall diel activity of fish in these littoral areas.

The temporal structure of fish communities, particularly diel patterns, has received less attention than other structural components such as trophic and spatial patterns (Helfman 1978). Studies of diel distribution patterns and fish behavior have generally examined differences between macrohabitat categories (e.g., littoral and limnetic zones) within lakes (Baumann and Kitchell 1974, Bohl 1980, Carlander and Cleary 1949, Keast and Welsh 1968). Few studies consider differences between adjacent littoral habitat patches, yet field and theoretical ecology continue to demonstrate the role of habitat heterogeneity in structuring populations and communities.

Differences should exist between the diel behavior of fish and habitat heterogeneity. Differences in resource availability between habitats (Ivlev 1961) and concurrent differences in fish association patterns (Larkin 1956, Werner and Hall 1977) suggest that energetic benefits from given strategies of diel behavior are not equal in all habitats. One strategy may yield high net returns of energy in one habitat, but in another net energy returns may be low with the same strategy. No studies specifically treat these ideas with respect to diel behavior, but the general topic of fish-habitat energetics has been examined by others (Glass 1971, Werner and Hall 1974, 1979, Werner, Mittelbach, and Hall 1981).

Two studies suggest the existence of within-habitat differences in fish diel activity. Helfman (1979a) noted within-population variation in diel activity patterns of yellow perch (*Perca flavescens*). He suggested that they may be due to genetic variation, fixed patterns of response to environmental conditions that differ between areas, or overall generalist adaptation of fish to historically varying environmental factors. These environmental factors included photic condition, predation pressure, food availability, water clarity, twilight length, and lake size. Hall et al. (1979) noted that a variable fraction of a golden shiner (*Notemigonus crysoleucas*) population underwent offshore diel migrations on different dates, and no diel separation occurred in their feeding on littoral and planktonic prey.

Our study examines several questions raised by these two investigations. Specifically, we focused on whether or not the same fish species, and size classes within those species, exhibited significantly different patterns of diel activity and association between different but adjacent littoral habitats. Differential patterns of diel activity and association may indicate adaptive behavior of fish in response to a locally heterogeneous environment.

STUDY SITE AND METHODS

This study was conducted on Utah Lake (Fig. 1), a large, shallow lake in north central

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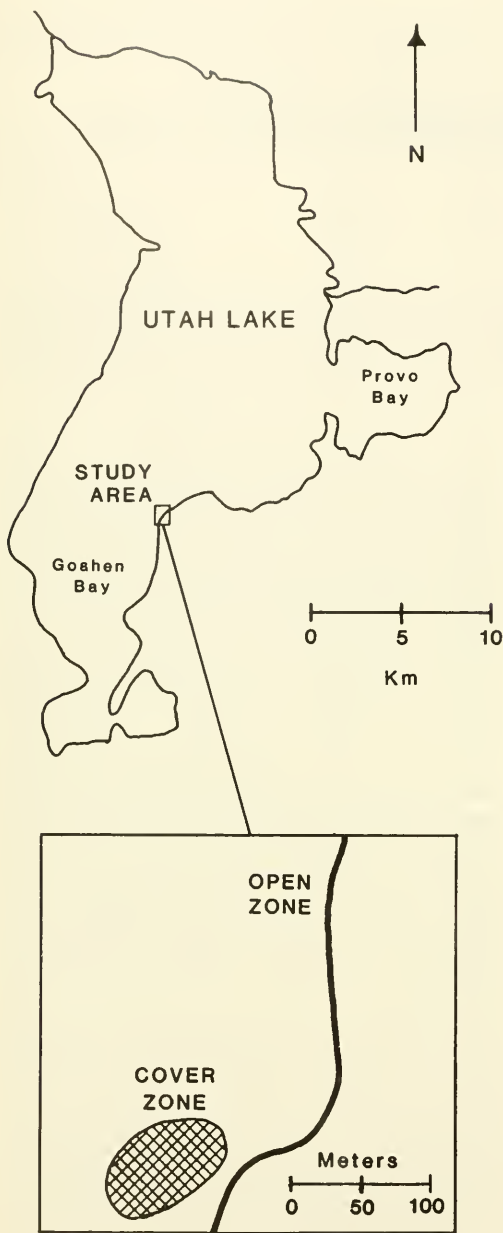


Fig. 1. Utah Lake (top) and the study site at Goshen Bay (bottom), showing the two habitat areas.

Utah approximately 25 km south of Salt Lake City. The lake has a surface area of approximately 38,000 ha, a mean depth of 2.9 m, and a maximum depth of 4.2 m. Utah Lake is described as being eutrophic, turbid, and slightly saline (Fuhriman et al. 1974). The water exhibits a high sulfate and carbonate content (Shiozawa 1975), and marl is being

actively deposited in several shoreline areas. Conductivity levels range between 500 and 1700 micromhos (mean 1200). Secchi disk readings are between 12 and 50 cm (mean 24 cm) (Shiozawa and Barnes 1977). Water temperatures range from 0 C in winter to 30 C in summer, with temperatures decreasing rapidly in the late fall and increasing rapidly in spring. Utah Lake is usually covered with 10–15 cm of ice from mid-December to mid-February (Tillman and Barnes 1973). During ice-free months it is polymictic, and no thermal stratification occurs.

Most of Utah Lake has a mud-ooze substrate, but many littoral areas contain sand, gravel, rubble, clay, and hardpan. Rooted aquatic vegetation is sparse, and algal blooms occur in various areas of the lake, especially during late summer.

During August 1980 (August 4–5, 11–12, 18–19 and 21), fish were sampled over 24-hr periods from two adjacent habitat patches within the rubble-littoral zone along the eastern shore of Goshen Bay. Two trap nets with 15-m leads were concurrently placed within each habitat zone, and fish were removed at 4-hr intervals. Specimens from each pair of nets were then pooled and classified to species and length.

Open and Cover Zones

The open habitat zone (Fig. 1, bottom inset), comprised a 50-m stretch of shoreline containing a large rubble–small boulder substrate with a sand-gravel matrix. This area was devoid of rooted macrophytes and had a mean depth of 1 m and a maximum depth of 1.8 m. Beyond this depth the substrate was a mud ooze. The other habitat, the cover zone, was located 200 m south. It encompassed a stretch of shoreline containing thick reed growth separated at intervals by narrow channels. The substrate was a large rubble–small boulder composition, but it also contained a thick matrix of silt and mud. The mean depth within this habitat zone was .95 m, the maximum 1 m. Between these two areas there was a gradient of reed cover. Water temperature (at one-half maximum depth) during the study was 26.5 C in the open zone and 23.5 C in the cover zone. The conductivity level in both habitats was 1450 micromhos.

Trap nets were placed with leads and trap openings towards shore. In the open zone leads extended to shore due to the steep gradient. In the cover zone, nets were placed in channels between reed beds, but because of a more gradual slope the leads did not extend to shore.

RESULTS AND DISCUSSION

We assume that the differences in the proportion of fish caught between time intervals corresponded to differences in activity levels of the fish (Carlander and Cleary 1949, Lawler 1969, Scott 1955). Some fish species may detect or avoid a net more readily than others (Lawler 1969), and the rate at which nonmigratory fish are caught reveals their entire activity pattern, but the capture of migratory fish reveals only the intensity of their activity while in that area (Carlander and Cleary 1949, Scott 1955). The probability of capture of any given fish species may change with habitat, even if their activity remains constant. For instance, fish feeding in the open zone may utilize a foraging behavior different from that used in the cover zone (Ivlev 1961, Eggers 1977). This influences their probability of capture, and catch rates in each habitat may relate not only to fish activity, presence, and avoidance, but also to the pattern and speed of fish movement (perhaps a function of habitat structure). The use of proportions minimizes but does not eliminate this problem by emphasizing diel changes in percentages rather than numbers.

White bass (*Morone chrysops*) represented 70.5% and carp (*Cyprinus carpio*) 24.9% of the total catch. By habitat, white bass accounted for 72.4% of all fish in the open zone, and carp accounted for 24.4%. In the cover zone, white bass composed 66.4%, and carp made up 25.6%.

Three discrete size classes of white bass were considered. Size I white bass (young-of-the-year < 105 mm) composed 60.5% of that species. Size II white bass (juveniles and subadults, 105–205 mm) accounted for 16.1%, and size III white bass (adults, > 205 mm) represented 23.4% of the catch. Carp showed two discrete groupings. Size I carp (young-of-the-year, ≤ 160 mm) made up 15.4% of that species and size II carp (juveniles through

adults, > 160 mm) represented 84.6%. Only 7 carp between 161 and 349 mm were collected.

Walleye (*Stizostedion vitreum*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), black bullhead (*Ictalurus melas*), and Utah sucker (*Catostomus ardens*) were also caught, but collectively accounted for less than 5% of the total.

The fish communities in both the cover and open zones did undergo diel changes in activity. Comparisons within a designated fish size class for between-habitat activity will be termed diel activity patterns. Comparisons between different fish size classes or species will be termed diel association patterns. Differences in diel activity patterns of fish between habitat patches were tested using the Komolgorov-Smirnov, two-sample general distribution test for discretely ordered data. In such application the results are conservative (Gibbons 1976).

Total carp, size I carp, size II carp, total white bass, and size III white bass had no significant differences in activity patterns between open and cover zones (Table 1). However, size I and size II white bass had significantly different patterns of diel activity between the open and cover zones ($p = .01$ and $p = .025$, respectively). Open zone size I white bass activity increased from early morning (0600 hr) to midafternoon, but in the cover zone activity began later in the morning (1000 hr) and then rose to the midafternoon peak. Size II white bass peaked in activity in the late afternoon (1800 hr) in the

TABLE 1. Results of tests for between habitat differences in activity patterns of white bass and carp.

	Open zone vs. Cover zone Level of significance (p-value)
White bass	
All sizes	NS
Size I	.010
Size II	.025
Size III	NS
Carp	
All sizes	NS
Size I	NS
Size II	NS

NS = nonsignificant.

open zone but in the cover zone activity levels peaked in the morning (0600 hr).

Patterns of diel association between fish classes were tested with Spearman's coefficient of rank correlation. Total white bass vs. total carp had no significant diel association patterns in either the open or cover zones. White bass sizes II and III were significantly negatively associated with carp ($.029 < p < .051$, Table 2) in the cover zone.

Variation between sampling days for both activity and association patterns was examined using loglinear models in categorical data analysis. No significant day to day variation in diel activity patterns existed for total white bass or total carp. Significant day-to-day variation occurred in the size I, II, and III white bass. In particular, day 3 was significantly different ($p = .012$) than the other days of the study. This difference occurred between late morning (1000 hr) and early afternoon (1400 hr). Day 3 (August 18) was the only stormy day sampled. The storm represented distinctly different environmental conditions and likely was the cause for the difference in activity patterns observed. Loglinear analysis of day-to-day variation in association patterns between white bass and carp also indicated that day 3 was significantly different within the cover zone ($p = .011$), with more size II and size III being present.

Between-habitat differences in diel activity of size I and II white bass and in diel association of white bass with carp may be caused by the following factors: (1) lateral migration (Emery 1973, Keast 1978, and Nursall 1973), (2) offshore migration (Baumann and Kitchell 1974, Hasler and Bardach 1949, Scott 1955),

(3) differential foraging behavior (Pyke, Pulliman, and Charnov 1977, Vinyard 1980, Werner and Hall 1976, Werner and Hall 1979), (4) differential patterns of intraspecific temporal resource partitioning (Hobson 1968, Scott and Crossman 1973), and (5) differential patterns of interspecific temporal resource partitioning (Collette and Talbot 1972, Helfman 1978, Helfman 1979b).

Lateral Migration

Higher frequencies of size I white bass were caught in both habitat zones at 1400 hr on day 3 of sampling (August 18–19). Activity levels for size I white bass in the open zone reach a peak earlier in the day (1000 hr vs 1400 hr) and those in the cover zone later (1800 hr vs 1400 hr), when day 3 is removed from the analysis. Size I white bass in the open zone decrease in activity in the afternoon (1400 hr to 1800 hr); concurrently they significantly increase their activity in the cover zone. In the littoral of Goshen Bay, lateral migration of size I white bass into the cover zone at night would be reinforced by the diel activity patterns of their dominant predator, the walleye (see Helfmann 1979a, Werner et al. 1977, viz., predation and the use of refugia by small fish). Walleye were only collected in the open zone and only at night and early morning, with the majority being captured after dark.

Rank correlation between adult walleye and size I white bass in the open zone showed a significant negative association by time ($r^2 = .017$, $p = .029$). Size I white bass have high activity levels during the day within the open zone, but are absent or inactive in that zone at night, the time when walleye are present. Utah Lake walleye also feed on young-of-the-year (size I) carp (Arnold 1960, Dabb and Thompson 1976). Size I carp, like white bass, decrease in activity at night within the open zone as their activity increases within the cover. Rank correlation between walleye and size I carp within the open zone showed no significant diel association, but this is largely due to a midday activity decrease for the carp.

Lateral migration may also occur for size II white bass, but the pattern is not conclusive. Size II white bass increase activity in

TABLE 2. Results of tests for diel association between white bass and carp.

	Correlation coefficient 4 Day Totals
Open zone	
All sizes white bass vs. carp	0.100
Size II and III white bass vs. carp	0.214
Cover zone	
All sizes white bass vs. carp	-0.085
Size II and III white bass vs. carp	-0.786*

* = significant at $.029 < p < .051$

the open zone later in the morning and cease activity later in the evening than the size I white bass. Size II white bass lengths were usually over 140 mm, and Utah Lake walleye seldom select white bass exceeding 120 mm in length. This size refuge eliminates predation constraints imposed on the predation-susceptible size I white bass.

Offshore Migration

Hall et al. (1979) noted that young-of-the-year golden shiners (*Notemigonus crysoleucas*) did not participate in the evening offshore migration for that species; however, Kelso and Ward (1973) showed that yellow perch fry (*Perca flavescens*) did migrate offshore during the day. The gear types and net mesh used in this study prevented us from making quantitative determinations of offshore movements for size I white bass (also see Hasler and Bardach 1949, Scott 1955, concerning sampling gear inefficiency on small fish); but, based on the trap net data, a complete offshore migration is not likely since size I fish numbers do not drop to zero in either zone.

Size II white bass undergo both lateral and offshore movements. Gill nets set perpendicular to shore (to detect lateral movement) were only slightly lower in catch-per-unit effort compared to gill nets set parallel to shore (to detect offshore movement).

Differential Foraging Behavior

Zooplankton were dominant prey items for size I white bass from both open and cover zones (Devine, unpublished data; see also Dabb and Thompson 1976, Trapnell 1969). Zooplankton densities were approximately equal in both habitat zones (Devine, unpublished data). Thus, if a feeding advantage exists in one habitat zone, it should relate to factors other than food density. If size I white bass are more successful in foraging within the open zone, a morning migration from the cover to the open zone could optimize their food intake (Baumann and Kitchell 1974).

Intraspecific Resource Partitioning

Partial correlation coefficients between white bass size classes were lower in the cov-

er zone than the open zone. Cover zone size II white bass dominated in activity in the early morning, and size I white bass dominated during the afternoon and early evening. Size III white bass were most active during late night and predawn hours. In the open zone a single size class seldom dominated activity. These differences may relate to the habitat structure of the two zones. The open zone, with an absence of reed beds, a steeper slope, and a greater average depth, provided more activity volume per unit of surface area than the cover zone. The compressed activity space within the cover zone may necessitate temporal partitioning of resources by the three size classes of white bass (see Werner and Hall 1977, viz., competition and activity space).

Interspecific Resource Partitioning

Size II and III white bass and carp exhibited no association by time in the open zone, but were significantly negatively associated within the cover zone. Carp had no significant difference in diel activity between the two zones. The white bass size II and III activity differences may relate to the avoidance of carp. Adult carp are primarily benthic feeders (Miller et al. 1959), although they do surface feed (McCrimmon 1968). White bass are primarily planktonic feeders (McNaught and Hasler 1971, Olmstead and Kilambi 1971), but may forage on benthic resources (Dabb and Thompson 1976, Trapnell 1969). Carp are aggressive feeders (Miller et al. 1959), and are much larger than the white bass.

In the cover zone less activity volume was available. White bass and carp, thus brought into closer proximity, would interact more intensely. If competition occurred for space, white bass are at a disadvantage due to their smaller size. Other studies document interference between fish (Janssen 1974, Werner and Hall 1977), but none mention an unintentional effect due to size and feeding behavior. White bass, if displaced by carp in the cover zone, could adjust their behavior through a number of mechanisms, including migration or movement out of the channels. Size I fish had an evening overlap, with carp in the cover zone, but the danger of walleye

predation in the open zone at this time may override the disadvantage of interacting with carp (see Werner et al. 1977). Spatial segregation of white bass and carp could more easily occur in the open zone because of the greater depth.

CONCLUSIONS

The patterns of diel activity and association of dominant fish species and size classes in this littoral community were different between habitat zones. Predation forced small fish into cover for protection during the night when the main predator, the walleye, was most active. Different foraging efficiencies between cover and open zones may act to draw these fish from the cover zone into the open zone during the day. Fish that were too large for predators interacted on the basis of inference competition. Carp with their disruptive foraging behavior could displace white bass in the cover zone because of the restricted space (due to reeds and shallowness). The open zone was deeper and lacked the narrow horizontal dimensions of the cover zone. It allowed spatial segregation of carp and white bass, and therefore no interference displacement occurs.

ACKNOWLEDGMENTS

We thank the following for assistance during this project: James R. Barnes and C. M. White for review of manuscript drafts; Melvin W. Carter aided in statistical analysis; and Paul Brown, Mark Martin, Dave Ng, Dan Plater, and Eric and Aaron Jessen provided volunteer help with the field work. The Utah Division of Wildlife Resources supplied the trap nets used.

Funding was provided by a research grant from the Brigham Young University College of Biological and Agricultural Sciences, No. 2-52817 to DKS.

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